THE TRACHEAL SUPPLY IN THE CENTRAL NERVOUS SYSTEM OF THE LARVA OF CORYDALIS CORNUTA L.

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This study was begun with two main objects in view. First, to determine some land-marks for use in a study of the finer structure of the ganglia and nerve cells of this insect; and second, to determine the exact air supply of each ganglion for the purposes of later experimentation.

It is well known that all of the organs of insects are abundantly supplied with tracheae and many fine tracheoles, but the number and dense arrangement of the minute tracheoles in many of the organs comes as a surprise to the person who sees them under a microscope for the first time. The central nervous system is no exception to other organs, indeed the tracheoles are very abundant in all parts of the nervous system.

One of the disputed points in regard to the tracheae is the question whether the minute tracheoles anastomose with each other or not. They are very abundant, they branch to some degree and they are very long and wind and twist themselves into such a dense mat that it is very hard to follow individuals and hard to tell whether they unite or not.

There seems to be very little literature on the tracheal system of Corydalis. N. Young Burke, in an unpublished thesis in the library of the Department of Entomology of Cornell University, shows the main tracheae of the tracheal system of Corydalis. In her figures, ventral transverse tracheal branches running from side to side are shown. It is from these ventral transverse branches that most of the ganglia are supplied.

The subesophageal ganglion has two branches which come from the transverse ventral eephalic trachea and run to the cephalic part of the ganglion on either side. This ganglion is also supplied by two other branches, one on either side in its caudal region. These come from another source more caudad of the ganglion.

The three thoracic ganglia all receive two branches, one on each side from a ventral transverse trachea, which like the tracheal branch of the upper part of the subesophageal ganglion come to the ganglia from a cephalic direction. The first to the seventh abdominal ganglia are supplied by one tracheal branch on each side, but these come to the ganglia from a caudal direction because the transverse tracheae in every case cross below or caudal to the ganglion to which they send branches. The transverse tracheae of the abdominal region except the first, are smaller as a rule than those of the thoracic region and the branches which run to the abdominal ganglia are often of considerable length.

The eighth abdominal ganglion is supplied from the outside by two long tracheal branches which come to it from the caudal direction.

The brain as described by Krauss '84, was found to be supplied by three lateral branches on each side from a common trunk.

The following pages will give a more or less detailed description of the tracheal supply in each of the ganglia of Corydalis.

For the larger branches ordinary dissection under a lens was the method of study. For finer details the entire central nervous system was removed and mounted in glycerine to which a drop of formalin was added. These mounts cleared up in a short time, the air in the finest tracheal tubes remained and they could easily be followed. No sections were studied at this time, but later, a large series of preparations will be examined with several objects in view, among them the determination if possible of how the finest tracheoles end.

THE BRAIN.

The brain is supplied by three main branches on each side, all of which come from a large eephalic tracheal branch. These three seem to be lateral portions from the large common trunk which runs forward somewhat reduced to supply other parts of the head.

The three trunks on each side, furnish each lateral half with all of its main tracheal branches. (Fig. A and 2.) There are comparatively few tracheae that cross the middle line and most of these are small. These three main portions enter the brain by their branches laterally from the ventral side and the description of them will be given as though they were seen from the ventral side.

The most cephalic part is the smallest and the most caudal the largest as a rule. Each part has both superficial and deep branches, and although the territories of the divisions overlap to some degree, the areas supplied by each are somewhat as follows: (1) *Cephalic branch*, dorsal and lateral portion including branches that go to the optic nerves. It divides into two main parts before entering the brain, a cephalic smaller branch which divides into a number of long tracheae, many of them superficial and supplying the latero-cephalic portion of the brain. The larger more caudal part of four or more rather large branches, for the most part deep ones which supply the central part of the brain and to some extent the other side.

(2) The middle branch, supplies deep parts to some degree, particularly in the latero-caudal region near the connective, including a large trunk which runs down it nearly to the subesophageal ganglion. On entering the brain this large middle branch divides into a number of deep portions.

(3) The caudal branch, gives superficial tracheae to the whole mesal half of the brain and deeper ones which penetrate the ventral side of the ganglion near the middle line at the caudal edge. It is of two main parts, the shorter portion which divides again soon into a number of branches near the middle part of the brain and a longer more ventral portion. Each of these main branches on running to the ventral side of the brain divides into tracheoles before entering, and the larger superficial, are easily seen from the ventral side, while the larger deep branches can often only be seen as they turn in to send deep tracheoles to the central part of the brain and smaller superficial branches to the dorsal side. The large superficial ventral branches send off many fine superficial tracheoles which may be seen over all parts of the brain, in some degree parallel to larger when larger branches are near.

In the center of the brain on each side, there was found a much darker area due to the mass of tracheoles which formed a central dense tuft. (Figs. A, G, & 1 & 2.)

Following the arched nerve on each side there is a small tracheal branch from the brain which supplies the small frontal ganglion, while on each side from some other lateral source a minute lateral branch also supplies this ganglion.

THE SUBESOPHAGEAL GANGLION.

The two pairs of branches supplying the ganglion are from two sources:

First, a ventral transverse tracheal branch of large size which runs across under the ganglion and a little above it. It sends off on each side a rather large tracheole which enters the ganglion at its cephalic and ventral surface. Second, two large branches which come from large lateral tracheae and run up to the lateral and ventral caudal edges of the ganglion.

The first, or more eephalic of these pairs of tracheae give off branches to the upper part of the ganglion. Upon entering, each divides at once into about two main parts and these short branches divide again into several and branches from these supply by both superficial and deep portions, the upper half of the ganglion, with a tracheole for each connective with the brain and small tracheoles to each of the nerves which come off in this region. The branches which go to the nerves and the connectives break up into a very fine network of tracheoles without anastomosis. In the case of the connectives, the area supplied is less than one half the length of the distance to the brain. The fine tracheoles in the connectives and the larger nerves run in a sort of circular or spiral manner. Many minute tracheoles are given off from all the branches in the ganglion.

The second or caudal pair of tracheae are larger than those just described. They come from long lateral branches from below. They supply the lower half of the ganglion, including the connectives, with tracheae and tracheoles. On entering the ganglion they each divide at once into about two main parts; the more cephalic portion of a number of branches which run towards the cephalic part of the ganglion. The other smaller portion consisting chiefly of a large branch which supplies the most caudal part of the ganglion with small tracheae and a large branch which supplies the connective of its own side by one very long twig and others shorter.

Superficial and deep branches form a dense network throughout the ganglion. There seem to be about as many small trachcoles in the middle line as at the periphery. Branches from one side cross to the opposite side in considerable numbers. Branches from the upper and lower supplying trachae interlace considerably. There are many long fine tubules with few side branches, few free ends, and no anastomoses. Although the trachcoles are abundant in all parts of the ganglion, the densest mass of them is in the central part, on each side.

The longest connective branches from the lower tracheae run only about one third of the length of the connectives between this ganglion and the first thoracic. The connectives between these two ganglia are very long and their middle portion is supplied on each side by a tracheole not connected directly with the tracheal system of either, but from an outside source. The tracheal system of the connectives is very complete, many fine long branches wind and interlace about the connectives with few free ends and no anastomosis, although the long fine branches of different systems mingle very intimaetly. (Fig. B, H & 3.)

FIRST THORACIC.

This ganglion is supplied by a transverse branch above it much like that supplying the cephalic part of the previously described ganglion. From this transverse branch or rather arch. branches one on each side enter the ganglion laterally and a little toward the head end. There are two main branches given off at once on each side. On the left side the more cephalic is in large part a connective branch, which divides into two at the cephalic part of the ganglion; the outer of these runs up the outside of the connective for a long distance and its branches mingle with those of the median independent branch of the connective. The inner of the two just mentioned, runs to the point of origin of the cephalic connectives and sends a somewhat smaller branch along the inner side of each connective as well as a few short tracheoles which turn back into the ganglion, between the connectives. Both of these inner and outer connective branches send a number of supplying tracheoles to the upper third of the ganglion. On the left side the more caudal portion runs into and along the edge of the ganglion, towards the caudal connectives, distributing branches to the lower part of the ganglion and sending a few short branches to the connective of its own side. On the right side the larger more cephalic branch is quite different. Similar parts of the ganglion are supplied by it as by the most cephalic branch of the left side, only there seem to be more branches and there is only one small connective twig which runs on the outer side of the connective of the right side. The more caudal branch of the right side is more like its fellow of the opposite side in the number and position of the branches. In addition, a large recurrent portion was traced way up almost to the origin of the cephalic connective of the same side.

The above is a description of the main branches of the first thoracic in a single specimen. Variations of this were found in other specimens, particularly in the cephalic and caudal regions of the ganglion in relation to the connectives. The supply of the

cephalic connectives was more often nearly symmetrical and in a number of specimens there was an additional median supplying branch to the ventral region of the ganglion. This median supplying branch ran under the ventral side of the ganglion, or a little distance caudad of it on the connectives. It was found to be fully as large as one of the branches of the lateral supply. about half of the specimens this branch was found and was apparently torn off in one or two of the other specimens. This unpaired branch divides into three a little below the ganglion, the two lateral tracheae run up to the base of the ganglion, one on the dorsal side, one on the ventral side and each breaks up into numerous tracheoles about the base of the ganglion near the middle line. The median branch runs also in a cephalic direction for a short distance and then divides into two and these again into two main parts on each side, the more cephalic portion bends out and after breaking into a number of smaller tracheac, supplies the more caudal and lateral parts of the ganglion, while the more caudal portion bends back with few twigs to supply the connective. (Fig. 4.)

The various larger branches mentioned in connection with this ganglion each give off an intimate supply of fine tracheoles, both superficial and deep and although a certain area has more tracheoles from a particular trunk, there are also numerous tracheoles winding in all directions from other systems. The area within the ganglion which receives the best supply of fine tracheoles is the central part on each side. The median line is rather clear because there are few branches in this region, although a number of the tracheoles from both sides cross this area in every direction. (Fig. 4.)

SECOND THORACIC.

In a similar way to the first ganglion a branch on each side enters from the transverse abdominal tracheal trunk. These two branches run down laterally and to the ventral and slightly cephalic region of the ganglion.

On each side the supplying trunk divides into three main portions. A cephalic, consisting of a single long branch to the outer side of the connective and a small tracheole from this which runs more medially on the cephalic connectives. A median part which breaks up into about five branches to supply the central and cephalic part of the ganglion and a caudal branch. This caudal portion is much smaller on the left side and furnishes small tracheoles to the internal, lateral and caudal portions of the ganglion, but not much to the connective. The right corresponding branch, however, is large and besides supplying tracheae to the ganglion gives off two main parts which supply the caudal connectives.

Variations from the above description were found in other individuals studied. In some the supply to the ventral connectives were symmetrical, or chiefly from the left side. The supply of the cephalic connectives although more uniform was sometimes less symmetrical. And the cephalic connectives were often supplied at their origin by branches from a number of systems. (Fig. C. and 5.)

As in previous ganglia the nerves were each supplied by usually one small branch, each from the nearest tracheal system. The distribution of the smaller tracheoles was much like that in the first thoracic ganglion.

THIRD THORACIC.

The tracheal supply is much the same in this as in the previous ganglion.

In the specimen of the series most described as a basis for the larger branches, the left hand caudal branch instead of the right hand one furnishes most of the connective supply. (Fig. D, and 6.)

FIRST ABDOMINAL.

In the thoracic ganglia, the ventral transverse tracheal branch which sends out two tracheae to each ganglion crosses above or cephalic to the ganglia. The transverse tracheal branches supplying the next seven, cross caudal to the ganglia which they supply.

The first abdominal ganglion is much like the others in its main branches. In the series most described and figured the cephalic connective supply is symmetrical, the caudal supply mostly from the left. In other specimens mostly from the right with now and then a slightly less symmetrical distribution in the cephalic region. This ganglion and the following show a more definite lateral localization of the fine branches. (Fig. D and 7.)

SECOND ABDOMINAL.

Similar to the first. The main trunks come to it more medially. On the right side of the one of the series, the lower or caudal connective is the larger. (Fig. 8.)

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THIRD ABDOMINAL.

Similar. More medial supply. Quite a symmetrical distribution of branches in all specimens studied. (Fig. 9.)

FOURTH ABDOMINAL.

Very similar to the last. In the type specimen there is an additional inner supply to the cephalic connectives from the left. (Fig. 10.)

FIFTH ABDOMINAL.

Similar to the others. In the specimen described, the left cephalic connective mostly supplied from the left side. The caudal from the right. (Fig. 11.)

SIXTH ABDOMINAL.

Nearly symmetrical in regard to the cephalic and median branches in the type, although the left is a little larger. The caudal connectives supplied largely from the left. (Fig. 12).

SEVENTH AND EIGHTH ABDOMINAL.

The seventh ganglion has quite a symmetrical distribution. The most cephalic branches on either side run up the connectives, each on its own side. Two main central parts give tracheoles to the main part of the ganglion, while a very large caudal part on each side runs down the connective with a few short branches to it and then breaks up into two main parts to supply the upper portion of the eighth ganglion, although branches run way down to the very tip of the ganglion as well. Two other main trunks come to the eighth. Two rather large tracheae run up from the caudal and lateral tracheal trunks to enter the ganglion ventrally and laterally. These two last, differ from the other supply of the other ganglia in not being connected with a ventral transverse tracheal branch. Each of these last mentioned breaks up into four or five main trunks and these supply the lower two thirds of the ganglion as well as the numerous nerves which take their origin from this region. (Fig. F and 13.)

The conditions just described for the Eighth abdominal ganglion are very uniform.

As may be seen from the description of the individual ganglia of larval Corydalis, special branches are the only ones which supply the central nervous system with air. These special branches are three on each side to the brain from a large cephalic branch; two pairs to the subesophageal ganglion, the cephalic coming from the ventral transverse connecting branch, the eaudal from the lateral tracheal tubes below the ganglion; one pair supplying the middle part of the connectives between the suboesophageal and the first thoracic; one pair supplying the first thoracic and one unpaired to the same ganglion; one pair to each of the remaining thoracic and one pair to each abdominal ganglion. The last ganglion receiving two branches from the caudal region as well as two large branches from the system of the seventh.

The tracheae of the central nervous system of Corydalis larva seem to be uniformly as outlined above, and the branches which supply the nervous system come directly from large tubes and these in most cases take their origin not far from spiracle openings in the thoracic region and from very near the gills in the abdominal region.

The larger branches in the ganglia are quite uniform in the distribution of their smaller tracheoles. There was found to be a greater variation in the connective branches in the same individual and in the ganglia of one specimen as compared with an other. The supply to the connectives however, was quite uniformly given by the tracheal systems of the ganglia at either end of the connectives. The only variations were the constant ones; first, in the additional extra supply to the long connectives between the sub-oesophageal and the first thoracic ganglia; second, in the supply to the connectives between the seventh and eighth abdominal ganglia, where the tracheae from the seventh ganglion furnish the connective branches.

All nerves connected with the ganglia were found to have a good tracheal supply, usually one rather small tracheole which branched many times and here as in the connectives, the branches wound about without anastomosis and without any particular indication of the direction of the nerve fibers, that is transverse as well as longitudinal branches were numerous.

The branching of the smaller tracheae from the larger was rather irregular and the course and distribution of the finest branches was very complex. Within the ganglia as a rule fewer larger branches were seen. On the surface, and each side of the middle line dense masses of tracheoles outlined the central part of the ganglion. But although there were these two dense tangles one on each side in each ganglion, numerous minute, and some larger branches erossed from one part of the ganglion to an other distant region and mingled with the branches from other systems. The small branches within the ganglion run straight or in broad curves to a considerable extent, while the finer branches in the connectives are often wavy. (Fig. M. & N.)

A few ends were found, but no clear case of anastomosis either between systems or between branches of the same system, although it looked like it in many places because of the great length and intricate windings of the finest tracheoles. From the smallest tracheoles also there were comparatively few branches although single ones could be traced for long distances.

The connectives gave a good chance to study the distribution of the finer branches and their relation to each other. Here although two systems overlapped, no anastomosis could be found. (Fig. L.)

SUMMARY.

1. There is a very intricate and extensive supply of both tracheal branches and capillaries to the central nervous system of Corydalis larva.

2. There are three main branches to the brain on each side, entering it laterally and ventrally.

3. There are two pairs of branches to the subesophageal.

4. There are three branches, two paired and one unpaired, to the first thoracic ganglion.

5. There is but one pair of branches to all the other ganglia except the eighth.

6. The eighth ganglion has two sources of tracheae. Two branches from the seventh abdominal ganglion and two from the caudo-lateral region of the animal.

7. The supply to the connectives in all cases but one, is from the tracheal systems of the ganglia.

8. The supply to the long connectives between the subesophageal and first thoracic ganglion is in part from both of these ganglia and its middle portion is supplied by a small lateral tracheal tube.

9. Nerves supplied by only one small tracheole may have this forming a very complete network.

10. The frontal ganglion is supplied from the brain on each side along the small connective and also from two small lateral tracheae not connected with the brain.

11. There is a superficial and a deep supply to each gauglion and a very intricate network in each.

In each ganglion, especially the abdominal, the central 12. area on each side is well marked by a dense tuft of minute tracheoles.

The large, and especially the small branches from one 13. system cross over to the regions of other systems to a marked degree.

14. Although minute tracheoles are long and fine, no anastomosis could be demonstrated.

Within certain limits the tracheal supply is regular and 15. constant.

The tracheae supplying the ganglia are rather directly 16. connected with the larger tubes, not far from spiracles in the upper region and very close to gills in most of the abdominal region.

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